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Abstract

Besides habitat loss and fragmentation, global warming is a major anthropogenic factor affecting species today. With temperatures rising, and barriers to movement increasing, many species are turning to behavioural responses deal with increased temperatures. These behavioural responses can be with respect to time or space use. However, with respect to such behavioural responses, animals have to manage the trade-off between food availability, predation risk and temperature. In this study I will look at how differently-sized herbivores respond to variation in temperature and predation risk while keeping food availability constant by using only grazing lawns in Hluhluwe-iMfolozi Park (HiP), South Africa. Camera traps and temperature sensors were used to monitor visitation and temperature on twenty-two grazing lawns across the park. Visibility analysis was also conducted to serve as a measure of horizontal cover or perceived predation risk. It was found that large bodied individuals, white rhino (*Ceratotherium simum*), were effected by temperature and responded temporally, where as small bodied individuals, impala (*Aepyceros melampus*), were effected by both temperature and predation risk with both a temporal and spatial response.

Global warming is currently affecting every ecosystem on the planet, from the hot dry deserts to the cold wet arctic. Global temperature averages are expected to increase a minimum of 2°C by the end of the century, with some models predicting up to 6°C (Hulme et al. 2001, Ogutu et al. 2007, Niang et al. 2014). Africa is expected to have a faster rise in land temperature than average, and South Africa expected to see drier winters with a later onset of rainfall than they are currently experiencing (Erasmus et al. 2002, Niang et al. 2014). Southern Africa is characterized by El Niño-Southern Oscillation (ENSO) which affects the precipitation (Ogutu and Owen-Smith 2003, Ogutu et al. 2007). The precipitation in turn effects the vegetation growth and therefore the population size of herbivores (Ogutu and Owen-Smith 2003). Global warming along with habitat loss and fragmentation are already the greatest threats to species today (Estes et al. 2011, Boyles et al. 2011, Shrestha 2012). With this change continuing, individuals that are specialized for the ecosystems that they live in will be expected to move, adapt or die (Lowe et al. 2010, Boyles et al. 2011). In many cases, moving is not an option due to barriers, so in order to survive an animal needs to adapt to the new circumstances that they live under. Yet, many large mammals have long life expectancies and generation times, so will not be able to adapt genetically quickly enough. Therefore they will have to deal with increasing temperatures through behavioural changes (Belovsky and Slade 1986, Hetem et al. 2012).

Large mammals have a smaller surface area to volume ratio than that of smaller mammals, as well as a thicker skin boundary layer (Phillips and Heath 1995, du Toit and Yetman 2005, Shrestha et al. 2014). Because of this, large mammals have a harder time with the rate of dissipating heat so are predicted to be less capable of dealing with extreme ambient temperatures outside their thermoneutral zone (TNZ) as the ability to dissipate heat becomes more difficult (Morgan 1998, Owen-Smith et al. 2005, Cain et al. 2006, Kinahan et al. 2007, Gardner et al. 2011, Boyles et al. 2011, Shrestha 2012). One would then predict large mammals to respond more strongly behaviourally to high ambient temperatures than smaller mammals. However animals can employ different strategies to cope with extreme temperatures (Phillips and Heath 1995, Gardner et al. 2011). These strategies can include behavioural strategies such as shifts in activity (temporal) times or spatial shifts to actively select cooler microclimates (ie. shade)(Maloney et al. 2005, Cain et al. 2006, 2008, Porter and Keraney 2009, Shrestha et al. 2012), orientate themselves to be parallel to the sun's rays (Maloney et al. 2005, Cain et al. 2008, Hetem et al. 2011) or involuntary responses like sweating and panting (Maloney et al. 2005, Cain et al. 2008, Shrestha 2012). Also it has been found in cattle that grazing and traveling creates three and five times more heat respectively compared to being idle (Shrestha et al. 2014), and direct sun can produce two to four times higher thermal loads than shade (Cain et al. 2008).

Many studies have looked at the temporal shift in activity levels with respect to temperature, in that during hot periods, animals shift to being more active at night and less active during the day (Belovsky and Slade 1986, du Toit and Owen-Smith 1989, du Toit and Yetman 2005, Maloney et al. 2005, Hetem et al. 2012, Owen-Smith and Goodall 2014). However very few papers, until recently, have looked at how changes in the selection of microhabitats could be a behavioural response to temperature extremes (McKechnie and Wolf 2009, Gardner et al. 2011, van Beest et al. 2012). Those that do

look at the selection of habitats in the African savanna do so on a large scale (Hetem et al. 2007, Kinahan et al. 2007, Knegt 2010, Shrestha et al. 2014).

Herbivores choose where to forage based on three main factors: food resources, predation risk, and temperature (Owen-Smith et al. 2005, Lowe et al. 2010, van Beest et al. 2012), with mainly resource availability and predation risk being studied to date (Cromsigt and Olff 2006, Burkepile et al. 2013, Shrestha et al. 2014). Trade-offs between these factors may occur when selecting the microhabitats in which an individual will forage that seems to be based on body size (Belovsky and Slade 1986, Owen-Smith and Goodall 2014). For example, an area that has a high nutrient content might also possess a high risk of predation, and the individual should then select an area with decreased nutritional content to ensure survival. When looking at the African savanna in the wet summer months, when food is not limiting but temperatures are high, herbivores should select for microhabitats based on temperature and predation risk. Following the relation between temperature and heat loss describes above, I predict that the trade-off between temperature and predation risk should differ between large and small herbivores. I predict that large herbivores should response more to variation in temperature than risk while smaller herbivores should response stronger to variations in predation risk (Sinclair et al. 2003, Estes et al. 2011). Cover can be an important factor when choosing where to forage as it has the ability to manipulate the temperature, predation risk, food availability, structure, etc. (Mysterud and Østbye 1999). Therefore the availability of cover should have an effect on all herbivores, as the cover provides shaded microclimates, but those microclimates also come with an increased predation risk as it provides predators with the ability to stalk their prey species (Mysterud and Østbye 1999). Other studies have noted that elephants selected for habitats that warm up and cool off at a slower rate than other sites in order to ease the transition to extreme temperatures, and this is also done through cover (Kinahan et al. 2007).

In this study, I will look at how African herbivores select microhabitats within their larger habitats with respect to temperature and predation risk. Moreover, I will look at only the grazers so as to control for feeding type effects on habitat selection. Specifically, I will look at the trade-off between temperature and predation risk for different body-sized ungulates ranging from megaherbivores, ie. white rhino (*Ceratotherium simum*), to small herbivores, ie. impala (*Aepyceros melampus*). I will also look at the relative importance of temporal versus spatial responses to variations in temperature. I predict that megaherbivores will be unaffected by predation risk, as they are rarely a prey species. However, megaherbivores will be affected greatly by temperature. Hence, I predict megaherbivores to be most active at night and avoid the hotter time periods. If active during the day, they will select for sites with low temperatures, while during the night they will use all microhabitats more evenly, due to cooler temperatures occurring across all microhabitats. Small sized herbivores on the other hand, will be strongly affected by predation risk, and less affected by temperature. Increased predation risk should prevent the smaller herbivores from completely shifting their activity to the night. Rather, they should select for the still relatively cool crepuscular periods. If active during the night, I predict that small herbivores will select for open areas at night to reduce the risk of predation. During the crepuscular period, I predict that small herbivores should use select for low risk sites over temperature, as it is

still relatively cool. Only during the hottest time period, day, should smaller herbivores be effected by temperature.

Methods

Study Site

This study took place in Hluhluwe-iMfolozi Park (HiP) in the KwaZulu-Natal province of South Africa. This is a state-run protected area of 90,000 ha in the southern African savanna biome, with habitat ranging from open grasslands, to closed *Acacia* and broadleaved woodlands (Cromsigt et al. 2009). There is a strong elevation and rainfall gradient across the park, with up to 1000 mm at high elevations and 650 mm at low elevations. Common grazing herbivores in the park include white rhinoceros, buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetes*), plains zebra (*Equus quagga*), impala, and warthog (*Phacochoerus africanus*). The study area has a highly seasonal climate with the most rainfall and highest temperatures occurring during the summer months (October-March)

Study Design

My study consisted of twenty-two grazing lawn sites distributed along gradients of canopy cover, and vegetative cover (figure 1, table 2). I only used grazing lawns because they are by definition high quality food patches (Hempson et al. 2014) which allowed me to standardize food availability across all plots. I assumed that the gradients of canopy cover and vegetative cover represented variation in temperature and predation risk respectively. Finally, I distributed plots across the park, as the park is heterogeneous in terms of landscape and rainfall.

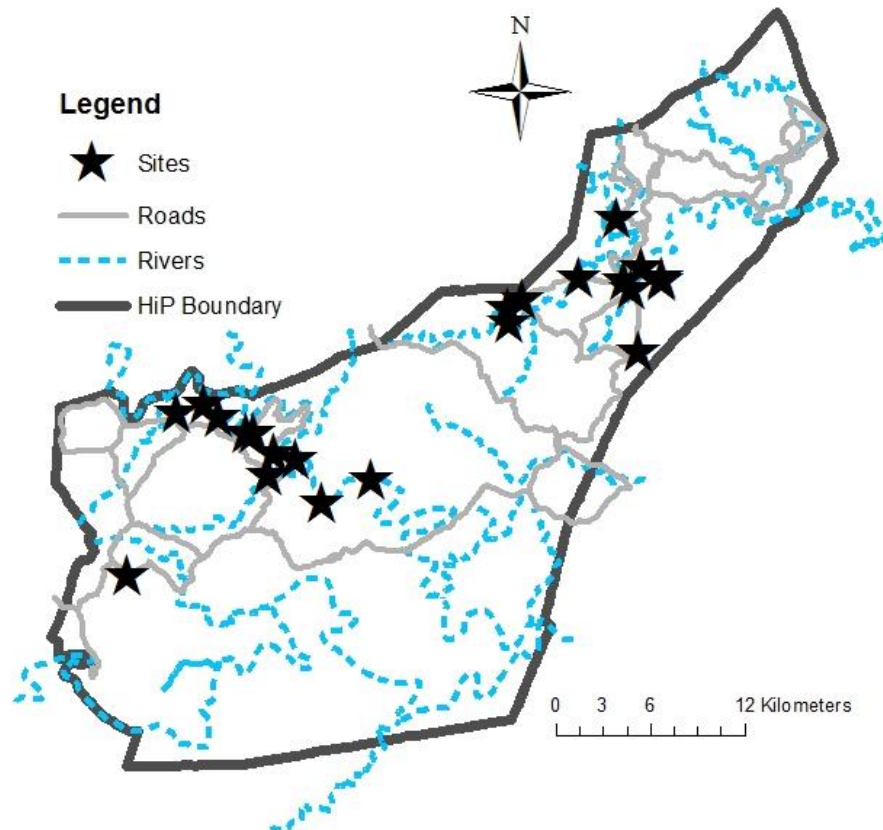


Figure 1. Map of the 22 sites (black stars) in HiP (boundary: dark grey line) with public roads (light grey line) and rivers (blue dotted lines).

Monitoring Sites

The technology used in this study was camera traps and iButtons. The camera traps (Bushnell Trophy Cam) were motion activated infrared cameras. iButtons are a Thermochron iButton device, DS1921G, used to measure and record ambient temperature. Each site once fully set up consisted of one camera trap and one iButton in a five by five meter plot. The camera was placed at the edge of the plot, to ensure the whole plot was photographed, and was placed at about 0.5m off the ground so animals of all heights could be photographed. The camera was set to be active continuously, taking pictures when triggered by movement with a lag time of one second between photos. The iButton was placed in the middle of the plot on a wooden pole, 0.25m off the ground, measuring the ambient temperature every fifteen minutes. Fifteen minutes was chosen as it allowed for fine scale temperature measurements and sufficient memory storage on the device. All iButtons were facing south in a plastic clip to allow for attachment with the metal side facing into the wood to control for the amount of sunlight that was actually on the sensor itself. I used the first several weeks of the experiment to test different ways of keeping the iButton in the middle of the plot and out of direct sunlight, as I wanted to measure the temperature the animals felt when foraging in the plot. I recorded visitation and temperature to all the plots during the wet season from November 2014 till March 2015. All the sites were visited weekly to do maintenance, ie. change batteries, SD cards, and iButtons, as well as to check that the iButton and camera trap were upright and still

functioning. Also the cameras were rotated between sites to control for any idiosyncrasies associated with individual cameras.

Vegetation Measurements

I measured the canopy cover using a spherical densiometer. Using the densitometer I estimated the average percentage of canopy cover across four directions (North, East, South, West) for each plot. I also did visibility surveys for each plot in March/April 2015. The visibility surveys acted as a measure of horizontal cover and a proxy for predation risk. This survey was done by having one person standing in the middle of the plot and another person walk a plank out in 8 directions (North, Northeast, East, Southeast, South, Southwest, West, and Northwest). The plank had marks on it to show 20, 40, 60, 80, 100, 120, 140, 160cm from the ground. The person walking the plank out would stop every meter for twenty meters, meanwhile the person in the middle of the plot would determine at which distance half of each section was no longer visible (ie. blocked by vegetation). This was done with the person in the plot standing at wildebeest height (120cm), impala height (90cm), and warthog height (60cm).

Data Analysis

White rhino and elephants regularly knocked down the poles/trees that camera traps, and particularly, iButtons were fixed to. While fieldwork was still occurring, I dropped one site because white rhino were constantly knocking over the iButton pole. At the end of the data collection period, another two sites were excluded from further analyses because sampling in these sites were too irregular due to the iButton and camera trap being knocked over. This left a total of nineteen sites that I used for further analyses (figure 1). Still, sites varied in the frequency of which rhinos and elephants knocked down the poles. Therefore, I calculated the number of days a site had been active monitoring by summing the number of days that the camera and iButton were in the right position and functioning for the entire day. In addition, any pictures that only had animals outside of the five by five meter plot were also excluded from the analysis so as not compound the visibility within a site with the visitation.

Only three grazer species had high enough visitation for detailed analyses (see appendix); impala, warthog and white rhino. Warthog were there further excluded they were only active during daylight, which did not allow me to compare temporal versus spatial responses for this species. Therefore for this analysis only impala and white rhino were used as they are active at all times of the day and are present in the same habitat across the park. The temperature and visitation were divided into four different time periods; dawn 3:00-9:00, day 9:00-15:00, dusk 15:00-21:00 and night 21:00-3:00. This division was chosen as day is the hottest time period, night the coolest and dawn and dusk fell in between the two, while keeping the same number of hours in each time period (figure 2). The visitation, defined as the number of photos taken per species per site, was summed for these time periods and the temperature had a mean, maximum, minimum and standard deviation calculated. For the temporal analysis this was done on a per time period per day basis meaning a sum for each time period per day, and for the spatial analysis this was done on a per site basis, meaning I summed across all days for each site.

I calculated the visibility to be a single number per plot by reassigning the height categories a number. The 160cm box was assigned the number one all the way to seven for the 40cm box, as lower height sections should carry more weight since it is these sections that would include predator that are stalking close in on their prey. The 20cm box was excluded all together, as the main predators in this system are taller than this, even when stalking. Also the boxes that were not half filled at 20 meter distance were assigned 25m. The single measure was finally obtained by multiplying the distance from the plot by the height measure, averaging those numbers and averaging the eight directions. Example measurement can be seen below in table 1. These were then assigned high (>90), medium (59-85) or low (<50) visibility according to the number calculated.

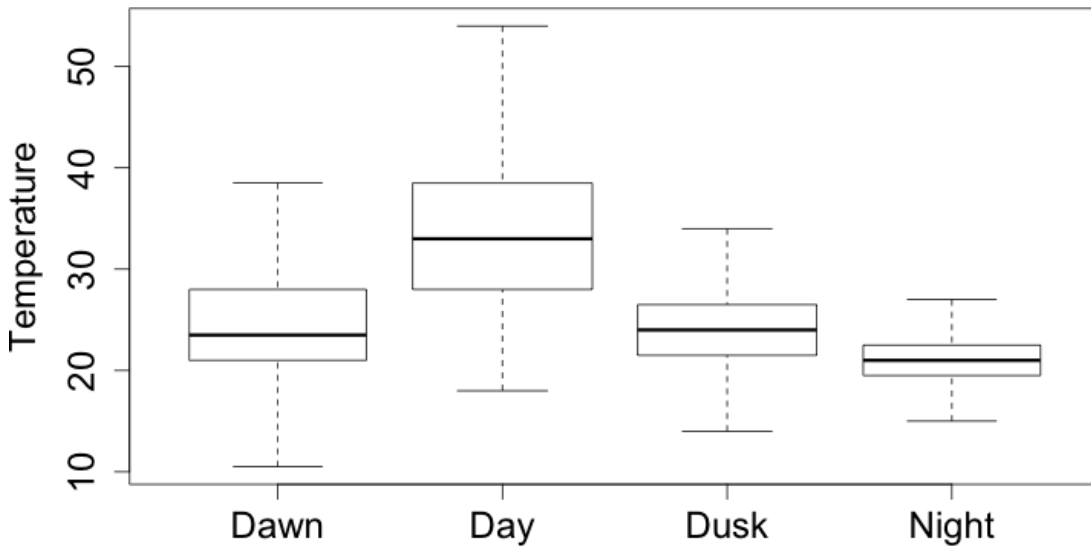


Figure 2. Temperatures by four time periods.

Table 1. Example calculation for visibility measure in one direction at one site.

| Height Category (cm) | Height Conversion | Distance Measured (m) | Distance Used | Multiplication | Summed Measure |
|----------------------|-------------------|-----------------------|---------------|----------------|----------------|
| 140-160 | 1 | >20 | 25 | 25 | 343 |
| 120-140 | 2 | 14 | 14 | 28 | |
| 100-120 | 3 | 14 | 14 | 42 | |
| 80-100 | 4 | 14 | 14 | 56 | |
| 60-80 | 5 | 13 | 13 | 65 | |
| 40-60 | 6 | 13 | 13 | 78 | |
| 20-40 | 7 | 7 | 7 | 49 | |
| 0-20 | Excluded | 7 | | | |

Statistics

All statistics were conducted in R. First, I did correlation analysis for the sites characteristics; visibility, canopy cover and the mean temperature associated with that site. For the temporal analysis, I removed all time periods with zero visitation. I did this because I was interested in the shift in activity levels when they were active. Therefore by

removing days with zero visitation I only looked at when they were actually active, which time periods were they using. I then tested for the effects of time period (with four levels), temperature and their interaction by performing generalized mixed-effect models using the function glmer. This allowed me to include non-normal distributions and random effects. I compared model fits using AIC values for the different temperature variables to select the one that best explained variation in visitation. As a random effect I included date nested within site, to correct for repeated measurements per site. Also I used poisson models, since my visitation data was count data. For the spatial analysis, I summed all the daily minimum temperatures and daily visitations across the four time periods for each site. I then divided the summer daily visitation by the number of days active per site to get a per day average. To test for the effect of temperature and visibility, as a factor with three levels (high, medium, and low), I also tested for interactions between temperature and visibility. For both the temporal and spatial analysis, I ran pairwise post-hoc tests to test for differences in visitation among the different levels of time and visibility.

Results

Mean temperature differed by 2.6°C across my 19 sites (table 2) from November 2014 - March 2015 with the sites being active for 34 - 117 days. During this time, impala were photographed a total of 4415 times and white rhino 946 times. Temperature was not highly correlated with either type of cover; -38% and -15% for canopy cover and horizontal cover respectively (table 3). Therefore horizontal cover could be used as predictors independent of temperature.

Table 2. Site Characteristics. Impala and rhino visitation is the summed visitation for all active days

| Site | Canopy Cover | Visibility Impala/Rhino | Mean Temperature (Standard Deviation) | Impala Visitation | Rhino Visitation | Days Active |
|------------------------|--------------|-------------------------|---------------------------------------|-------------------|------------------|-------------|
| AIPO | 0 | 91/93 | 24.5 (6.8) | 109 | 44 | 54 |
| Ed. Center | 96 | 45/45 | 25.8 (7.1) | 11 | 18 | 102 |
| Exclosure | 0 | 98/100 | 25.5 (8.2) | 1015 | 0 | 80 |
| Gqoyeni | 82 | 62/63 | 25.6 (7.0) | 50 | 30 | 76 |
| Hlatikulu | 40 | 60/61 | 25.8 (7.4) | 331 | 4 | 117 |
| Madlozi | 0 | 84/85 | 25.4 (7.4) | 548 | 44 | 80 |
| Mansiya | 74 | 42/44 | 24.5 (7.1) | 0 | 57 | 62 |
| Mbhuzane | 0 | 81/85 | 25.8 (7.4) | 390 | 0 | 77 |
| Munyawanene | 96 | 83/83 | 24.1 (5.8) | 0 | 34 | 76 |
| Nomageje Closed | 5 | 49/46 | 25.5 (7.8) | 38 | 50 | 52 |
| Seme East | 0 | 100/100 | 24.3 (6.8) | 569 | 78 | 72 |
| Seme West | 0 | 84/85 | 25.1 (6.9) | 28 | 57 | 85 |
| Seven to Three | 84 | 59/62 | 25.0 (6.6) | 435 | 0 | 107 |
| Shooting Range | 19 | 45/48 | 25.7 (8.4) | 7 | 109 | 60 |
| Sontuli Closed | 0 | 27/28 | 26.0 (8.5) | 76 | 152 | 83 |
| Sontuli Open | 0 | 96/96 | 26.2 (7.8) | 461 | 87 | 101 |
| Thiyeni | 91 | 43/42 | 24.5 (5.7) | 0 | 0 | 108 |
| Thoboti | 0 | 77/77 | 26.7 (7.8) | 330 | 127 | 109 |
| Transect 24 | 26 | 41/44 | 25.7 (6.3) | 17 | 55 | 34 |

Table 3. Correlation matrix for how cover affects the mean temperature at each site, values determined using correlation in R.

| | Canopy Cover | Horizontal Cover | Mean Temperature |
|-------------------------|--------------|------------------|------------------|
| Canopy Cover | - | -0.42445 | -0.37997 |
| Horizontal Cover | -0.42445 | - | -0.14837 |
| Mean Temperature | -0.37997 | -0.14837 | - |

Temporal

The model with minimum temperature, best explained variation in visitation (table 4). Impala visited my grazing lawns more during the dawn and dusk period, more than day and night ($p < 0.001$; figure 3). For the day and night, as the minimum temperature increases, the visitation decreases, where as the visitation during the dawn and dusk periods slightly increase ($p < 0.001$; table 5). This shows a temporal shift to dawn and dusk during higher temperatures and an overall higher use of these time periods. White rhino, visited lawns more during the night than during other time periods ($p = 0.02$; figure

3). White rhino decreased the use of the night period with increased temperatures, where as the use of the other three time periods went relatively unchanged ($p=0.02$; table 6).

Table 4. Comparison of different models based on AIC values. Species is the visitation rate per species, time is the time periods and mean/max/min/StdDev are the temperature characteristics.

| Model | Degrees of Freedom | AIC Rhino | AIC Impala |
|---------------------------------------|--------------------|-----------|------------|
| Species ~ Time + (1 Site/Date) | 6 | 815.11 | 3376.2 |
| Species ~ Time*Mean + (1 Site/Date) | 10 | 805.25 | 3260.2 |
| Species ~ Time*Min + (1 Site/Date) | 10 | 812.44 | 3203.2 |
| Species ~ Time*Max + (1 Site/Date) | 10 | 806.19 | 3216.2 |
| Species ~ Time*StdDev + (1 Site/Date) | 10 | 814.69 | 3320.5 |

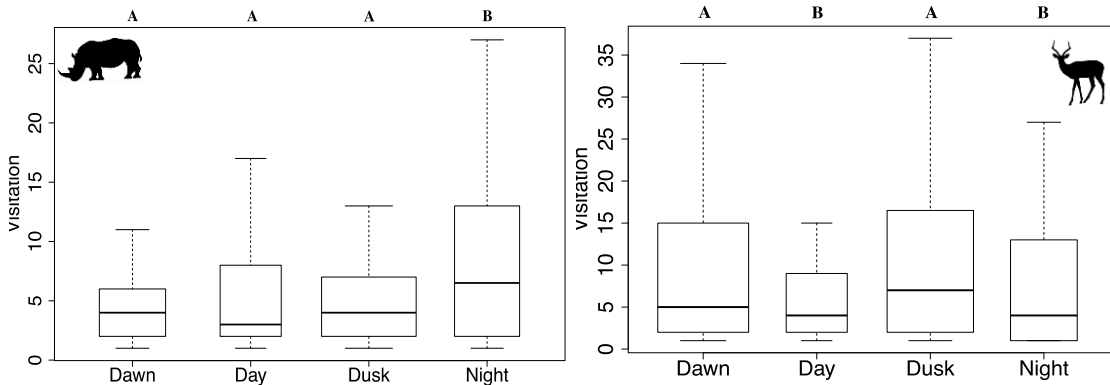


Figure 3. White rhino and impala visitation by time of day. Letters indication significance according to post-hoc pair-wise tests. Graph and statistics conducted in R.

Table 5. Summary statistics for impala visitation during four time periods according to the minimum temperature, values determined using generalized linear model in R, formula: Impala ~ Min*Time+(1|Site/Date), family: poisson, optimizer: Nelder Mead.

| | | Estimate | Lower CI | Upper CI | Posthoc Pair-wise Tests |
|----------------------|-------|----------|----------|----------|-------------------------|
| Intercept | Dawn | 0.977 | 0.261 | 1.693 | A |
| | Day | 4.515 | 2.987 | 6.043 | B |
| | Dusk | 0.375 | -1.174 | 1.924 | A |
| | Night | 4.320 | 2.670 | 5.980 | B |
| Slope of Temperature | Dawn | 0.026 | -0.009 | 0.060 | A |
| | Day | -0.115 | -0.188 | -0.043 | B |
| | Dusk | 0.071 | -0.004 | 0.144 | A |
| | Night | -0.113 | -0.196 | -0.031 | B |

Table 6. Summary statistics for white rhino visitation during four time periods according to the minimum temperature, values determined using generalized linear model in R, formula: Rhino ~ Min*Time+(1|Site/Date), family: poisson, optimizer: Nelder Mead.

| | | Estimate | Lower CI | Upper CI | Posthoc Pair-wise Tests |
|---------------------------------|--------------|----------|----------|----------|-------------------------------|
| Intercept | Dawn | 1.145 | -1.076 | 3.367 | A |
| | Day | 1.965 | -2.959 | 6.891 | A |
| | Dusk | 1.314 | -3.602 | 6.225 | A |
| | Night | 5.125 | 5.122 | 5.127 | B |
| Slope of Temperature | Dawn | 0.018 | -0.087 | 0.112 | A |
| | Day | -0.012 | -0.061 | 0.211 | A |
| | Dusk | 0.006 | -0.05 | 0.235 | A |
| | Night | -0.173 | -0.175 | -0.170 | B |

Spatial

The model best describing the data used visibility, time and temperature (table 7), with four time periods also being better than two. Impala used high visibility/low predation risk sites the most and low visibility the least ($p < 0.01$; figure 4). White rhino on the other hand used all sites evenly (figure 4). Impala during the night and dusk periods used sites with high visibility the most and low visibility the least (table 7, figure 5). During the dawn and day periods temperature had an effect on their choice, high visibility sites being used the most during low temperatures. As the temperature increased the different visitation classes became more uniformly used. White rhino had less of an effect with no selection for visibility (table 8, figure 6) with high scatter in the data, and using high and low risk sites rather evenly.

Table 7. Values used to determine model use for spatial analysis. Species is the visitation rate per species, time is the time periods, vis is the visibility class and min is the minimum temperature.

| Model | Residual Degrees of Freedom | AIC Rhino | AIC Impala |
|---------------------------------------|--------------------------------------------|----------------------|-----------------------|
| Species ~ Vis | 73 | -323 | -239 |
| Species ~ Vis*Time | 64 | -321 | -241 |
| Species ~ Vis*Time*Min | 52 | -311 | -251 |
| Species ~ Vis*Time*Min - Vis:Time:Min | 58 | -315 | -235 |

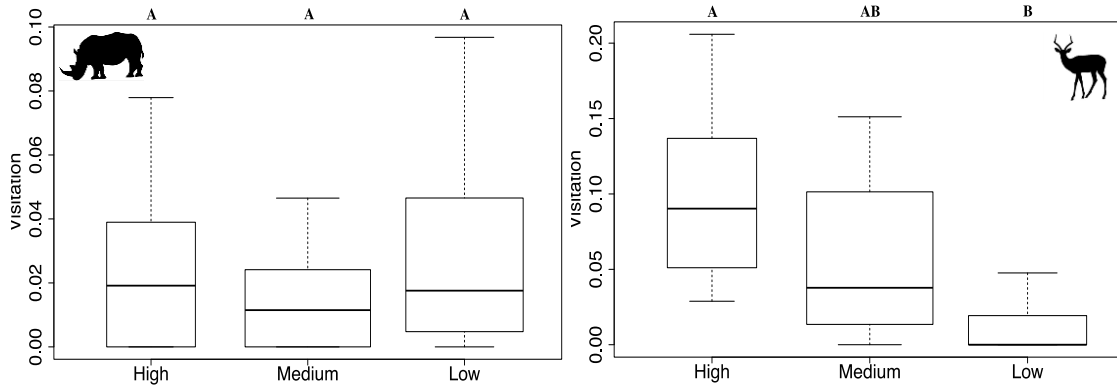


Figure 4. White rhino and impala visitation to sites of high, medium and low visibility. Letters indication significance according to post-hoc pair-wise tests. Graph and statistics conducted in R.

Table 8. Summary statistics for impala visitation during four time periods and three visibility classes according to the minimum temperature, values determined using a linear model in R, formula: Impala ~ Vis*Min*Time.

| | | | Estimate | Lower CI | Upper CI | Posthoc Pair-wise Tests |
|----------------------|-------|--------|----------|----------|----------|-------------------------|
| Intercept | Dawn | High | 5.65 | 3.34 | 7.95 | A |
| | | Medium | 1.44 | -4.27 | 7.15 | B |
| | | Low | -0.16 | -4.85 | 4.54 | C |
| | Day | High | 0.20 | 3.342 | 7.947 | A |
| | | Medium | -0.78 | -4.269 | 7.147 | A |
| | | Low | -0.34 | -4.851 | 4.534 | A |
| | Dusk | High | -1.13 | 3.343 | 7.947 | A |
| | | Medium | 0.073 | -4.268 | 7.147 | A |
| | | Low | 0.051 | -4.850 | 4.534 | A |
| | Night | High | -0.28 | 3.343 | 7.947 | A |
| | | Medium | 0.11 | -4.268 | 7.147 | A |
| | | Low | -0.03 | -4.85 | 4.534 | A |
| Slope of Temperature | Dawn | High | -0.27 | -0.389 | -0.16 | A |
| | | Medium | -0.06 | -0.352 | 0.216 | B |
| | | Low | 0.009 | -0.225 | 0.242 | C |
| | Day | High | -0.005 | -0.389 | -0.16 | A |
| | | Medium | 0.029 | -0.352 | 0.216 | A |
| | | Low | 0.012 | -0.225 | 0.242 | A |
| | Dusk | High | 0.06 | -0.389 | -0.160 | A |
| | | Medium | -0.00056 | -0.352 | 0.216 | A |
| | | Low | -0.0017 | -0.225 | 0.242 | A |
| | Night | High | 0.020 | -0.389 | -0.16 | A |
| | | Medium | -0.0037 | -0.352 | 0.216 | A |
| | | Low | 0.0016 | -0.225 | 0.242 | A |

Table 9. Summary statistics for white rhino visitation during four time periods and three visibility classes according to the minimum temperature, values determined using a linear model in R, formula: Rhino ~ Vis*Min*Time.

| | | | Estimate | Lower CI | Upper CI | Posthoc Pair-wise Tests |
|-----------------------------|--------------|---------------|----------|----------|----------|-------------------------|
| Intercept | Dawn | High | -0.929 | -2.23 | 0.377 | A |
| | | Medium | 0.801 | -2.427 | 4.037 | A |
| | | Low | -0.320 | -2.98 | 2.336 | A |
| | Day | High | -0.359 | 2.233 | 0.377 | A |
| | | Medium | -0.096 | 2.43 | 4.041 | A |
| | | Low | -0.268 | 2.984 | 2.336 | A |
| | Dusk | High | 0.756 | -2.233 | 0.377 | A |
| | | Medium | -0.45 | -2.43 | 4.041 | A |
| | | Low | 0.41 | -2.984 | 2.336 | A |
| | Night | High | -0.16 | -2.234 | 0.377 | A |
| | | Medium | 0.13 | -2.431 | 4.041 | A |
| | | Low | -0.033 | -2.985 | 2.336 | A |
| Slope of Temperature | Dawn | High | 0.048 | -0.017 | 0.113 | A |
| | | Medium | -0.04 | -0.201 | 0.1214 | A |
| | | Low | 0.017 | -0.113 | 0.1492 | A |
| | Day | High | -0.012 | 0.017 | 0.113 | A |
| | | Medium | 0.0037 | -0.167 | 0.121 | A |
| | | Low | 0.01 | -0.082 | 0.149 | A |
| | Dusk | High | -0.033 | -0.116 | 0.149 | A |
| | | Medium | 0.022 | -0.201 | 0.121 | A |
| | | Low | -0.016 | -0.116 | 0.149 | A |
| | Night | High | 0.009 | -0.017 | 0.113 | A |
| | | Medium | -0.0057 | -0.201 | 0.121 | A |
| | | Low | 0.003 | -0.116 | 0.149 | A |

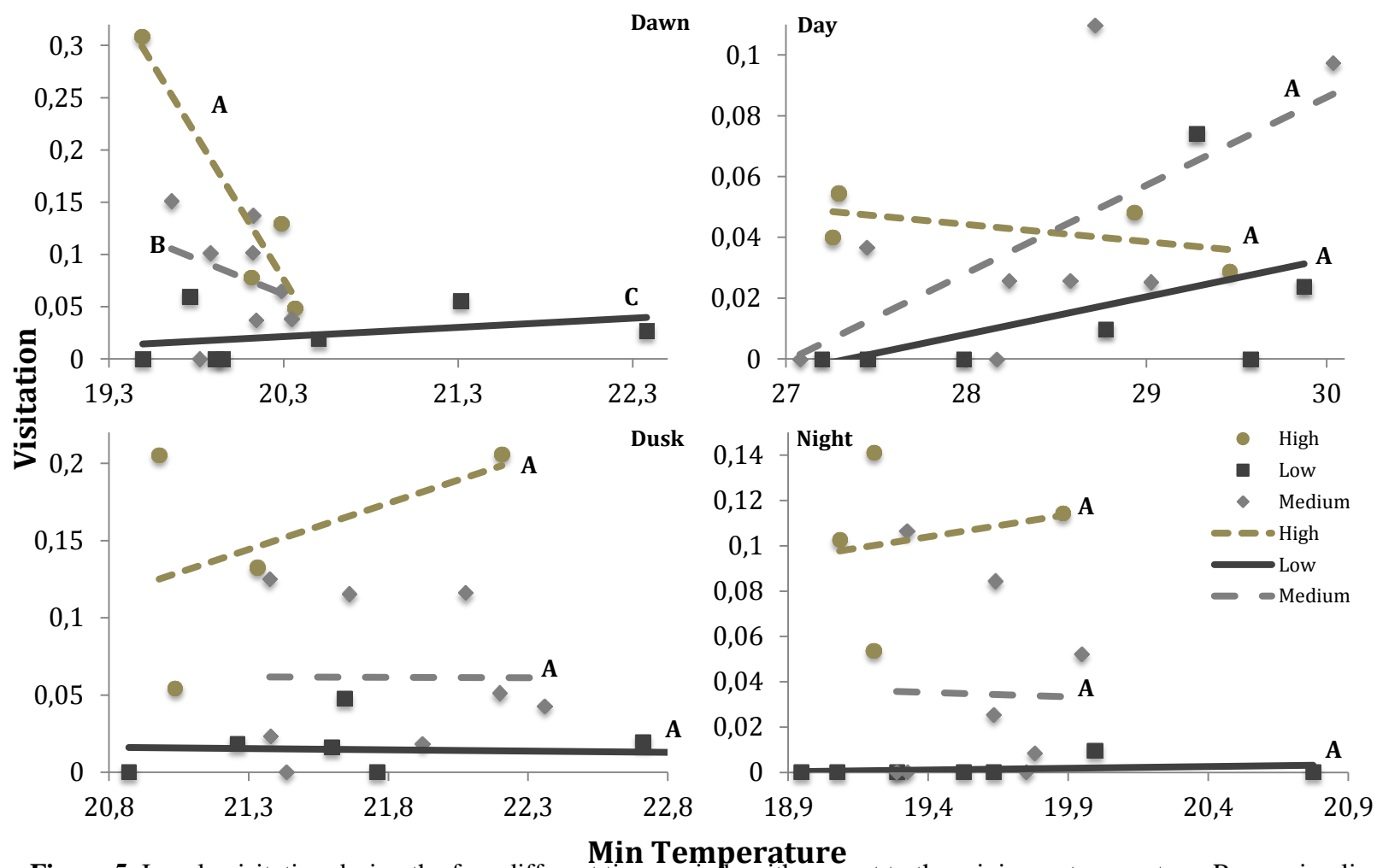


Figure 5. Impala visitation during the four different time periods with respect to the minimum temperature. Regression lines for the changes that occurs across high (gold), medium (light grey) and low (dark grey) visitation. Letters indication significance according to post-hoc pair-wise tests. Graphs in excel and statistics conducted in R, formula: $\text{Impala} \sim \text{Visibility} * \text{Time} * \text{Min}$.

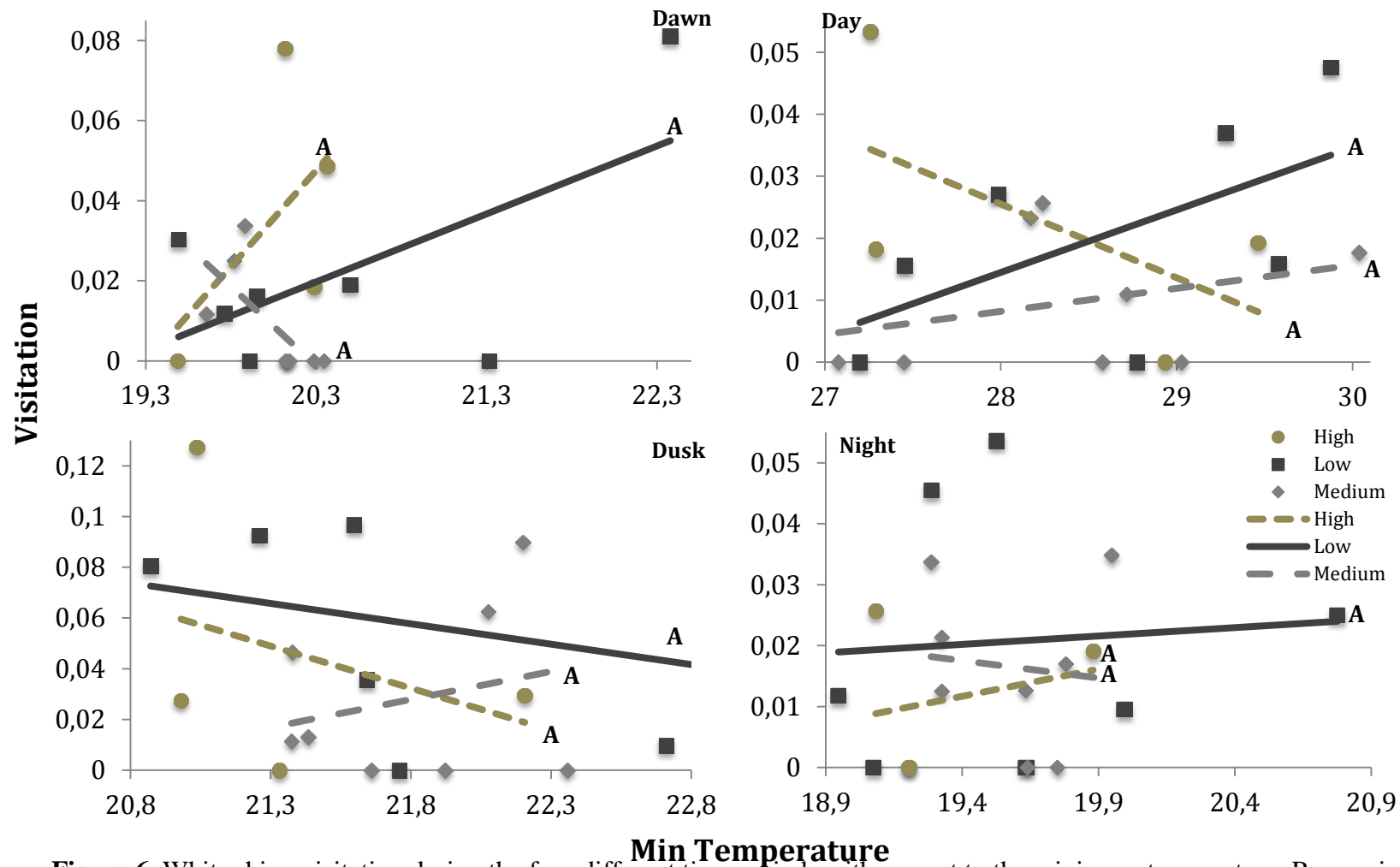


Figure 6. White rhino visitation during the four different time periods with respect to the minimum temperature. Regression lines for the changes that occurs across high (gold), medium (light grey) and low (dark grey) visitation. . Letters indication significance according to post-hoc pair-wise tests. Graphs in excel and statistics conducted in R, formula: Rhino ~ Visibility*Time*Min.

Discussion

The sites in this study varied in temperature, perceived predation risk and visitation by herbivores. A response in herbivores of different body sizes with respect to temperature and predation risk was detected. Large bodied species appeared to employ a temporal response to temperature, and did not seem to be affected by the spatial temperature aspect nor predation risk. Small bodied individuals exhibited both a spatial and temporal response to temperature with both being effected by predation risk.

Minimum temperature was used to evaluate how temperature effects herbivore habitat selection. Although this made sense by the AIC values, it also makes sense for biological reasons. The minimum temperature is more accurate than a maximum temperature, as, in summer, the maximum temperature is sensitive to momentary extremes, where as the minimum is more likely to reflect the overall temperature. Therefore a high minimum temperature will generally reflect a hot day better than a high maximum temperature. This is also a disadvantage of the iButton as it is metal, and if it is in the direct sunlight, it can heat up quickly. In this study, I did my best to control for this, but it further more makes the maximum temperature a less ideal measure.

Temporal shifts in activity have been widely recognized in the literature (Owen-Smith 1998, du Toit and Yetman 2005, Maloney et al. 2005, Cain et al. 2006, Hetem et al. 2012, Shrestha et al. 2014), and this study is no different. Although I only looked at the summer months, so I cannot see a shift in activity to the cooler times a day, as I have not winter data to compare it to, but for atleast the summer months, individuals appear to be selecting for the cooler time periods. White rhino used night more than any other any other time period by one and a half to two times more on average. This suggests that their large body size does cause more heat stress and they need to utilize the coolest time period (Phillips and Heath 1995, du Toit and Yetman 2005, Porter and Keraney 2009, Shrestha et al. 2014). Impala on the other hand used dawn and dusk significantly more than night or day. These time periods are also cooler, although not as cool as night. So, although they may have adjusted their temporal activity times according to temperature, they did not select for the coolest time period. As hypothesized in the introduction, this avoidance of night could reflect that predators are more active at this time. Lions (*Panthera leo*), leopards (*Panthera pardus*), and hyena (*Crocuta crocuta*) are mostly nocturnal causing this to be the most risky time period (Hayward and Kerley 2008, Crosmar et al. 2012, Burkepile et al. 2013). Impala and white rhino both showed a slight decrease in the use of day and night time periods with increasing temperature during these periods and a near zero increase in dawn and dusk. As I did not compare across the same day, but just looked at the time periods in general, this could be that they are less active on hot days overall as the decrease in day and night use was not supplemented by the slight increase in the dawn and dusk time periods (Belovsky and Slade 1986, Maloney et al. 2005).

In HiP, variation in grazing lawns in terms of the horizontal cover surrounding them provided different foraging options to the herbivores in terms of temperature and predation risk. Impala, as seen from the temporal analysis, already seen to avoid the riskiest time period: night. Moreover the sites ranged from open visibility to very limited visibility. The sites also ranged in their average temperature by 2.6 degrees. This heterogeneity in the grazing lawns allowed the herbivores to select the foraging sites with respect to their needs. Impala, a small-bodied herbivore used the open sites at low temperature much more than at high temperature. Also closed sites were used relatively evenly across all temperatures. Furthermore, only the low visibility sites were used at high temperatures, meaning that they could be selecting for the

riskier sites at high temperatures. White rhino on the other hand, were unaffected by predation risk. They used all the sites evenly, regardless of their visibility factor. This result can have further consequences for the trophic interactions that are happening, as white rhino appear to forage at all sites evenly, where as impala were selecting for sites. White rhino foraging effects would then be more evenly spread across the landscape, while impacts of impala should be more concentrated in selected safe and relatively cool areas.

In this study, only ambient temperature was used to measure how an animal experiences the temperature present. Although this has been shown to be the basic measure (van Beest et al. 2012), other things such as windy, humidity and radiation also effect the temperature that is experienced. However as research is normally constrained by funding and implementation in the field, I think the use of iButtons to measure ambient temperature can show a conservative estimate of how temperature is experienced. Although it can not be used to show absolute values.

In conclusion, this study suggests that impala, a small-bodied herbivore, experience a trade off between temperature and predation risk. However a mega-herbivore, white rhino, does not seem to experience this trade off and were only affected by temperature.

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Appendix

Table 9. Number of photographs per species at each site, all photos included.

| Site | Coordinates | | Cheeath | Hyena | Leopard | Lion | Wild Dog |
|-------------------------|--------------------|----------|----------------|--------------|----------------|-------------|-----------------|
| AIPO | 28.19462 | 32.03588 | 0 | 21 | 0 | 4 | 16 |
| Education Center | 28.25655 | 31.83902 | 0 | 1 | 0 | 0 | 0 |
| Exclosure | 28.22977 | 31.77020 | 0 | 3 | 0 | 0 | 0 |
| Gqoyeni | 28.25286 | 31.82627 | 0 | 3 | 0 | 0 | 0 |
| Hlatikulu | 28.26771 | 31.88223 | 0 | 21 | 0 | 6 | 0 |
| Madlozi | 28.32332 | 31.74212 | 2 | 11 | 0 | 4 | 0 |
| Mansiya | 28.11765 | 32.02270 | 0 | 0 | 1 | 3 | 0 |
| Mbhuzane | 28.23211 | 31.79497 | 0 | 0 | 0 | 5 | 0 |
| Munyawanene | 28.15875 | 32.03146 | 0 | 0 | 4 | 0 | 0 |
| Nomageje Closed | 28.14591 | 32.03693 | 0 | 2 | 2 | 0 | 0 |
| SemeEast | 28.15388 | 32.04909 | 0 | 7 | 0 | 1 | 0 |
| SemeWest | 28.16979 | 31.96055 | 0 | 2 | 0 | 0 | 0 |
| Seven To Three | 28.15330 | 32.02706 | 0 | 0 | 6 | 0 | 0 |
| Shooting Range | 28.17785 | 31.96165 | 0 | 5 | 2 | 7 | 0 |
| Sontuli Closed | 28.24088 | 31.81446 | 0 | 3 | 0 | 0 | 7 |
| Sontuli Open | 28.24137 | 31.81029 | 2 | 4 | 0 | 0 | 0 |
| Thiyeni | 28.15239 | 32.00154 | 0 | 3 | 1 | 0 | 0 |
| Thoboti | 28.22426 | 31.78649 | 0 | 21 | 0 | 6 | 0 |
| Transect24 | 28.26531 | 31.82255 | 0 | 12 | 0 | 0 | 0 |
| Grand Total | 28.19462 | 32.03588 | 4 | 119 | 16 | 36 | 23 |

| Site | Black Rhino | Buffalo | Elephant | Giraffe | Hippo | Impala | Kudu | Nyala | Warthog | Waterbuck | White Rhino | Wildebeest | Zebra |
|-------------------------|-------------|-------------|-------------|------------|-----------|--------------|-----------|-------------|-------------|-----------|-------------|-------------|------------|
| AIPO | 8 | 1117 | 9 | 34 | 0 | 1066 | 12 | 35 | 477 | 0 | 316 | 15 | 270 |
| Education Center | 0 | 1 | 53 | 0 | 0 | 93 | 13 | 17 | 15 | 0 | 63 | 11 | 0 |
| Exclosure | 0 | 50 | 614 | 0 | 0 | 4873 | 7 | 20 | 190 | 0 | 25 | 437 | 24 |
| Gqoyeni | 7 | | 98 | 6 | 0 | 269 | 1 | 17 | 61 | 0 | 124 | 3 | 0 |
| Hlatikulu | 3 | 4 | 27 | 0 | 0 | 658 | 0 | 80 | 0 | 0 | 0 | 0 | 0 |
| Madlozi | 81 | 51 | 32 | 9 | 0 | 5686 | 0 | 0 | 194 | 0 | 98 | 554 | 44 |
| Mansiya | 4 | 56 | 16 | 9 | 0 | 0 | 0 | 70 | 1 | 15 | 541 | 0 | 6 |
| Mbhuzane | 14 | 2 | 35 | 0 | 0 | 1280 | 0 | 16 | 20 | 0 | 28 | 2 | 0 |
| Munyawanene | 0 | 0 | 39 | 40 | 47 | 0 | 5 | 1029 | 21 | 0 | 78 | 0 | 27 |
| Nomageje Closed | 77 | 74 | 80 | 21 | 0 | 252 | 0 | 145 | 80 | 0 | 374 | 0 | 45 |
| SemeEast | 24 | 445 | 38 | 41 | 0 | 1454 | 0 | 0 | 6 | 0 | 436 | 273 | 358 |
| SemeWest | 0 | 453 | 59 | 17 | 0 | 230 | 0 | 0 | 9 | 0 | 200 | 4 | 56 |
| Seven To Three | 0 | 0 | 6 | 8 | 0 | 1145 | 0 | 271 | 53 | 0 | 14 | 0 | 0 |
| Shooting Range | 2 | 197 | 111 | 66 | 0 | 176 | 0 | 67 | 31 | 0 | 320 | 0 | 24 |
| Sontuli Closed | 0 | 0 | 89 | 0 | 0 | 70 | 0 | 16 | 35 | 0 | 279 | 0 | 0 |
| Sontuli Open | 109 | 0 | 8 | 0 | 0 | 1424 | 0 | 0 | 65 | 0 | 87 | 255 | 8 |
| Thiyeni | 9 | 0 | 60 | 33 | 0 | 0 | 0 | 495 | 12 | 0 | 5 | 0 | 0 |
| Thoboti | 32 | 27 | 47 | 0 | 0 | 914 | 0 | 31 | 543 | 0 | 229 | 8 | 2 |
| Transect24 | 2 | 0 | 97 | 10 | 0 | 443 | 9 | 6 | 38 | 0 | 463 | 27 | 5 |
| Grand Total | 372 | 2477 | 1518 | 294 | 47 | 20033 | 47 | 2315 | 1851 | 15 | 3680 | 1589 | 869 |

| Site | Aardvark | Baboon | Bird | Bush Pig | Duiker | Genet | Hare | Lizard | Mongoose | Monkey | Porcupine | Tortoise |
|-------------------------|-----------|------------|------------|-----------|-----------|------------|-----------|----------|------------|-----------|-----------|----------|
| AIPO | 0 | 0 | 6 | 1 | 13 | 0 | 34 | 0 | 0 | 0 | 0 | 0 |
| Education Center | 1 | 7 | 6 | 2 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 |
| Exclosure | 4 | 37 | 8 | 0 | 0 | 2 | 3 | 0 | 30 | 0 | 1 | 0 |
| Gqoyeni | 3 | 11 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 5 | 0 | 0 |
| Hlatikulu | 1 | 8 | 4 | 12 | 0 | 20 | 2 | 0 | 1 | 12 | 0 | 0 |
| Madlozi | 0 | 44 | 10 | 0 | 0 | 2 | 3 | 1 | 16 | 5 | 0 | 0 |
| Mansiya | 0 | 24 | 0 | 4 | 16 | 23 | 0 | 0 | 6 | 1 | 0 | 2 |
| Mbhuzane | 3 | 8 | 0 | 0 | 0 | 3 | 1 | 0 | 12 | 0 | 0 | 0 |
| Munyawane | 2 | 36 | 18 | 8 | 20 | 18 | 0 | 0 | 1 | 1 | 4 | 0 |
| Nomageje Closed | 0 | 22 | 0 | 7 | 8 | 6 | 0 | 0 | 3 | 0 | 0 | 0 |
| SemeEast | 3 | 10 | 28 | 2 | 1 | 1 | 14 | 0 | 19 | 0 | 13 | 0 |
| SemeWest | 0 | 6 | 0 | 0 | 1 | 0 | 0 | 0 | 11 | 0 | 0 | 0 |
| Seven To Three | 6 | 43 | 8 | 0 | 2 | 10 | 0 | 0 | 22 | 4 | 0 | 0 |
| Shooting Range | 0 | 72 | 2 | 26 | 0 | 6 | 0 | 0 | 2 | 8 | 0 | 0 |
| Sontuli Closed | 0 | 0 | 0 | 0 | 1 | 4 | 1 | 0 | 0 | 0 | 0 | 0 |
| Sontuli Open | 0 | 6 | 2 | 0 | 0 | 1 | 11 | 0 | 5 | 0 | 2 | 0 |
| Thiyeni | 0 | 0 | 37 | 4 | 16 | 20 | 0 | 0 | 0 | 6 | 0 | 0 |
| Thoboti | 3 | 40 | 2 | 0 | 0 | 5 | 5 | 0 | 2 | 0 | 2 | 0 |
| Transect24 | 0 | 3 | 0 | 13 | 10 | 4 | 0 | 0 | 1 | 2 | 0 | 0 |
| Grand Total | 26 | 377 | 131 | 81 | 88 | 127 | 74 | 1 | 133 | 44 | 22 | 2 |

SENASTE UTGIVNA NUMMER

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